

**BIOLOGY OF THE MYRMECOMORPHIC PLANT BUG
COQUILLETIA INSIGNIS UHLER
(HETEROPTERA: MIRIDAE: PHYLIINAE)**

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Abstract.—The basic biology of *Coquillettia insignis* Uhler (Heteroptera: Miridae: Phylinae) is described, including details of its growth, morphology, phenology, behavior and ecology. The distribution and abundance of this species over 20 sites in an eastern Oregon valley was studied, as well as its temporal and spatial relation to its host plant *Lupinus caudatus* Kell. Twelve species of ants were collected on *L. caudatus* of which six species were common; temporal, behavioral and morphological correspondence of these six species to various stadia of *C. insignis* are described. We identify several species of vertebrate and visual arthropod predators that could potentially serve as operators in the Batesian mimicry system to which *C. insignis* probably belongs.

Coquillettia insignis Uhler (Miridae: Phylinae) is a highly myrmecomorphic (ant-like) plant bug traditionally recognized as belonging to the tribe Hallodapini. This predominantly Old World tribe is comprised entirely of ant-like species and contains some of the most convincing morphological and behavioral 'mimics' of ants. With the exception of *Cyrtopeltocoris* Reuter, the New World genera of the tribe (*Coquillettia* Uhler, *Orectoderus* Uhler, *Teleorhinus* Uhler) and the Palearctic genus *Ethelastia* Reuter are now considered to form a monophyletic group distinct from other hallodapines (R. T. Schuh, pers. comm.). The less ant-like genus *Pronotocepris* Knight also seems to belong to this group, although its current placement is in the tribe Phylini (Carvalho, 1958).

Coquillettia is a North American genus comprising 22 species, all of which have females with remarkably ant-like appearance. Many species are very similar in external morphology and general coloration, making species recognition difficult. The lack of a comprehensive comparative study of the genus compounds the difficulty in obtaining accurate species identifications. Our determination of *C. insignis* for the present study was based on an examination of type specimens at the National Museum of Natural History, Washington, D.C. Although our study material was most representative of the type of *insignis*, we recognize that this species is highly variable as currently known, and that a careful comparative study of *insignis* and related species may alter the existing classification and nomenclature of the group. From our study of museum specimens and literature records (Carvalho, 1958 and included references; Kelton, 1980), it is evident that *insignis* is widely distributed in western North America (Fig. 1). It is typically associated with plants of the genus *Lupinus* L., but also has been reported (by label data) feeding on *Astragalus* L. and *Oxytropis* DC.

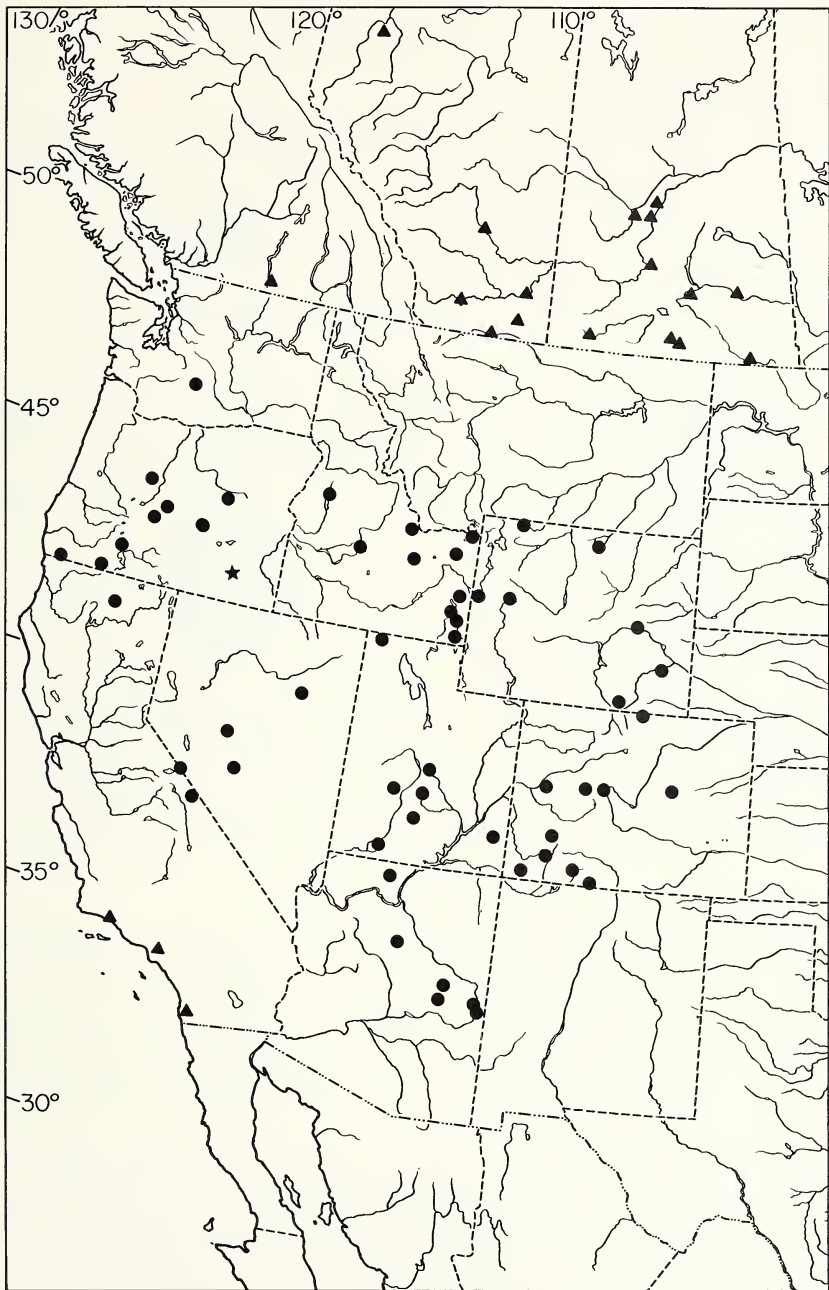


Fig. 1. Distribution of *Coquillettia insignis* Uhler: ●, records from our examination of museum specimens; ▲, other published records (also reported from the Dakotas, Kansas, Montana, and Texas but with no specific locality data); ★, Pike Creek study area in southeastern Oregon.

(other Fabaceae) in Colorado and Wyoming. In the Great Basin, adults are sometimes collected on sagebrush (*Artemisia* spp.).

The adults of *insignis* are sexually dimorphic, with the female being totally apterous and strongly ant-like (Fig. 2). The major myrmecomorphic features of the female include: 1) aptery; 2) elongation and lateral rounding of the thoracic tergites, especially the pronotum; 3) bulbous, petiolate abdomen with the anterior three segments strongly constricted and the lateral margins (connexiva) abruptly upturned; 4) large, elongate head with greatly enlarged gular region (Fig. 3); and 5) long, narrow legs. The adult male is macropterous and much less ant-like (Fig. 4), lacking all of the thoracic and abdominal modifications of the female, except the weakly constricted anterior abdominal segments.

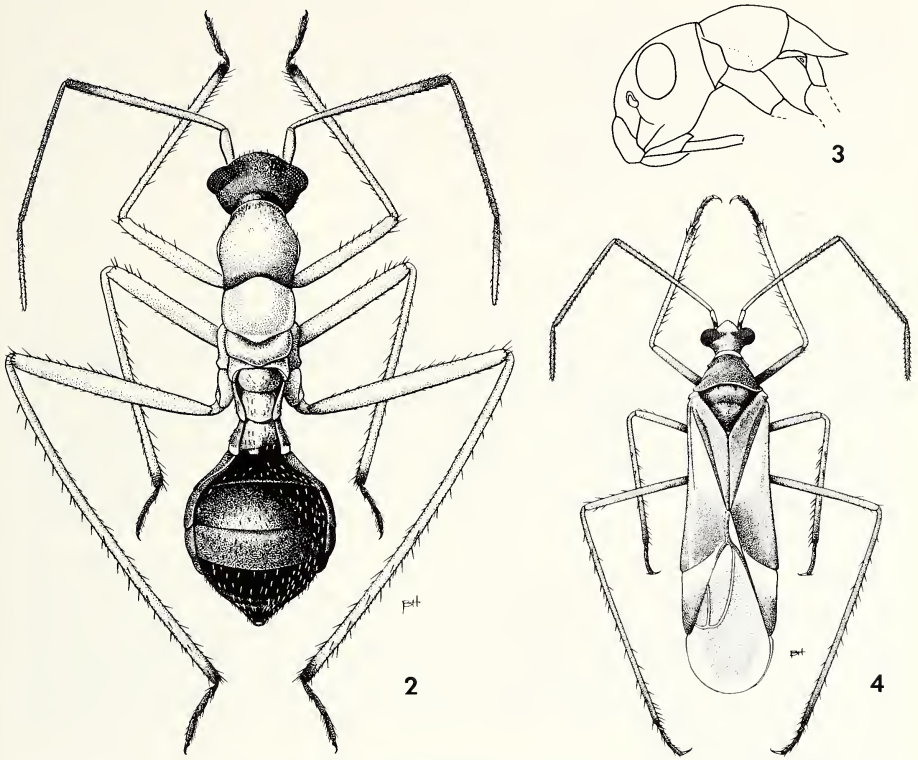
The nymphs of both sexes are good myrmecomorphs (Fig. 5), exhibiting many of the morphological attributes seen in the adult female. Late instar males are somewhat less ant-like due to growth of the meso- and metathoracic wing pads. Nymphs and adults of *insignis* have a pale, transverse band on the posterior margin of abdominal tergite III (both ventral and lateral surfaces) that may serve to enhance the petiolate appearance of the abdomen.

Although *Coquillettia* species are among the most convincing of myrmecomorphic insects, details on their basic biology and ecological relation to ant models and to potential operators are virtually unknown. *Coquillettia insignis* is an ideal candidate for the study of ant-mimicry because it is easy to sample, easy to maintain in the laboratory, and is relatively host-specific on lupine, allowing accurate identification of the arthropod community within which it interacts. This paper describes the basic biology of *insignis* and identifies the common arthropod species associated with it, including ant models and potential operators. This study, in conjunction with a similar treatment of *Orectoderus obliquus* Uhler (McIver and Stonedahl, 1987), will serve as a base upon which more detailed studies of ant-mimicry will depend.

METHODS AND MATERIALS

Study area. The research was conducted in June 1984 and May through August 1985 on the east escarpment of Steens Mt. in southeastern Oregon (118°32'30"W; 42°32'30"N). *Coquillettia* populations were studied at 20 sites along an altitudinal gradient from 1,353 m to 2,286 m (4,400–7,500 ft), within the Pike Creek drainage system. From these 20 sites, five primary sites were selected for intensive study (GBL, GBH, PLAT, CONF, HILL) (Fig. 6). Most of the specimens used for various aspects of the study were taken from these five sites.

Although varying in altitude (1,577–1,775 m), aspect (ESE-facing to SSW-facing) and slope (0° to 40°), plant communities of all primary sites were similarly dominated by sagebrush (*Artemisia tridentata* Nutt.), rabbitbrush (*Chrysothamnus nauseosus* (Pall.) Britton) and greasewood (*Sarcobatus vermiculatus* (Hook) Torr.), with a variety of herbaceous species intermixed (Great Basin Province, after Franklin and Dyrness, 1973). Since *C. insignis* was typically found only on *Lupinus caudatus* Kell., we focused our attention on this widely distributed species of erect, perennial, small-flowered lupine. The selection of study sites and the duration of the study allowed us to examine *Coquillettia* biology over its entire range within the Pike Creek drainage and over the entire active portion of its life cycle.



Figs. 2-4. Adults of *C. insignis*. 2. Female, dorsal habitus. 3. Female, lateral view of head. 4. Male, dorsal habitus.

Methods. Individuals representing all active stages of *Coquillettia* were collected in the field for description and illustrations. Some of these were reared on a lupine diet to obtain estimates of instar duration at ambient field temperatures (1-25 June 1985). Since temperature patterns throughout June were fairly constant (range of highs: 25°-32°C; range of lows: 8°-14°C), the instar duration estimates are good relative indicators of stage longevity. Eighteen field-collected and ten laboratory-reared females were dissected to obtain estimates of fecundity.

Sustained field observations were made of *Coquillettia* behavior on its host plant. Observations of continuous behavior were dictated onto a cassette tape recorder, and time budgets constructed for each set of observations. Casual observations of behavior were made throughout the season to supplement the time budget data. We observed behavioral activity for 3rd, 4th, and 5th instar nymphs, as well as for both sexes of adults. These data were compared with similar observations made on *Orectoderus obliquus* Uhler (another myrmecomorphic hallocladine) and *Lopidea* nr. *rolfsi* Knight, a nonmimetic plant bug.

Distribution of *C. insignis* was examined on a geographic scale (using information from the literature and museum collections), over the twenty Pike Creek sites, and

among individual plants at each primary site. Local dispersion patterns are described for the within-site data among individual plants.

Relative abundance, expressed as frequency per plant, was compared over primary sites (on each sample date) and within sites over time. Each sample consisted of five 50-sweep subsamples representing approximately 25 lupine plants. From these data we calculated a 'deme development index'—

$$\left(\sum_{i=1}^6 n_i \cdot i \right) / N,$$

where i = instar; n_i = # individuals at stage i ; N = total # individuals—starting at population peak and running through the remainder of the season for each of the five primary sites. This index provided an indication of the effect of elevation on the initiation and speed of postembryonic development in *insignis*.

The phenology of *L. caudatus* was monitored by recording size, condition, and degree of development for a set of lupine plants at the HILL, CONF, and GBH sites through June and early July 1985. This information allowed us to make inferences on the extent to which *Coquillettia* individuals distribute themselves according to these three plant properties.

At 5-day intervals from 1 June through 3 July 1985 (peak *Coquillettia* season), sweep-net and beat-sheet samples were taken from lupine at the CONF and PLAT sites to identify co-occurring ant species and the arthropod predator fauna. A list of possible avian and lizard predators observed foraging on lupine was also made. This information on potential models (ants) and operators (visual predators) is necessary for further studies on the nature of the tripartite Batesian mimicry system to which *Coquillettia* may belong.

RESULTS AND DISCUSSION

The life cycle. Overwintered eggs of *insignis* begin hatching in early to mid-May (at about 1,525 m elevation), and first instar nymphs can be found in the field until about the third week of June. Despite this wide temporal range in eclosion, most eggs hatch within a 10-day period in late May and early June. All nymphal instars of *insignis* are active, feeding stages. The durations of the five nymphal stadia, as determined by laboratory rearing, averaged 4.25, 5.12, 6.67, 6.05, and 7.71 days, respectively (Table 1). Total developmental time from first instar to adult averaged 29.86 days. Only field-collected specimens that appeared newly eclosed were used to determine stadium duration for the first instar nymph. Temporal range and peak abundance of nymphal and adult stages show *insignis* to be a 'June' species.

The phenology of *Coquillettia* tends to coincide with that of its host plant, *L. caudatus* (Fig. 7), which undergoes substantial vegetative growth starting in late April and continuing through May and early June. By early June (beginning of peak *Coquillettia* season), over 50% of the available lupine plants at GBL had flowered, while fewer than 10% had set seed. By 10 June, 74% of all plants at the same site had flowered or set seed and by 17 June, 90% had flowered or set seed. Plants decline in condition after the third week in June, with 100% of the individuals senescent at the lower sites (GBL, GBH, PLAT) by 6 July. *Coquillettia* tends to be associated with

Table 1. Duration (in days) of the nymphal instars of *C. insignis*.

Instar	N	Days		
		Range	$\bar{x} \pm SE$	Cum. mean age
1st	2	4.0, 4.5	4.25	4.25
2nd	4	4.5–5.5	5.12 \pm 0.25	9.43
3rd	6	3.0–11.0	6.67 \pm 1.15	16.10
4th	19	3.5–11.0	6.05 \pm 0.51	22.15
5th	21	4.0–11.0	7.71 \pm 0.40	29.86

plants of younger than average age, greater than average size, and better than average condition (McIver, pers. obs.). These observations of association between *Coquillettia* and *L. caudatus* suggest that *Coquillettia* individuals discriminate between plants of variable quality, an observation consistent with its herbaceous habit.

Whereas males disappear by the third week in July, females continue ovipositing until the second week in August. Ovipositional behavior was observed only once in the laboratory, with a female depositing eggs under the outer woody layer of a sagebrush stem. The female probed with her proboscis for several minutes at a single spot on the stem and then brought the ovipositor down on the probed area. The ovipositor was then gradually worked into the stem by flexing the entire abdomen along the longitudinal axis and by flexing the ovipositional muscles. The rear legs were suspended in the air during this process. When the ovipositor was embedded in the stem to within 1 mm of its base, the female stopped movements for 10 to 12 seconds and then quickly withdrew. Although this behavior was repeated three times, it is unlikely that *insignis* oviposits on sage in the field, as females are rarely collected on *Artemisia*. The preferred oviposition sites are probably the dried out, persistent lupine stems, a habit consistent with that observed for *O. obliquus* (McIver and Stonedahl, 1987). Eggs overwinter under the outer layer of dried stem tissue, and nymphs emerge in mid-May to early June to complete the life cycle. Whether *insignis* enters diapause is not known.

Fecundity estimate. A total of 28 adult females were dissected to determine egg load. Ten of these were reared from 5th instars and were dissected as virgins 2 days after the final molt. Average number of eggs for these females was 12.1 ± 2.7 (95% conf. interval), ranging from 7 to 20. Average egg load for 18 field-collected females was 14.7 ± 2.2 , with a range from 10 to 30. All eggs dissected from mature females were relatively large (1.0–1.3 mm) and appeared in most cases to be fully developed. The egg load usually occupied the entire bulbous portion of the abdomen and was especially tightly packed into the dorsal half of the abdominal cavity. Given the large volume of the egg load and the similar stage of development of all eggs in the ovaries, it is likely that *Coquillettia* produces only a single cohort of eggs, which are laid over a 4–6-week period. If this is the case, then our determination of egg load should be an accurate estimate of total fecundity. However, we have no conclusive evidence that *Coquillettia* does not develop subsequent cohorts of eggs.

Description of immature stages. EGG (Fig. 5a). Length 1.30–1.50 (all measurements are in millimeters), greatest width 0.19–0.22; gently curved with weakly constricted

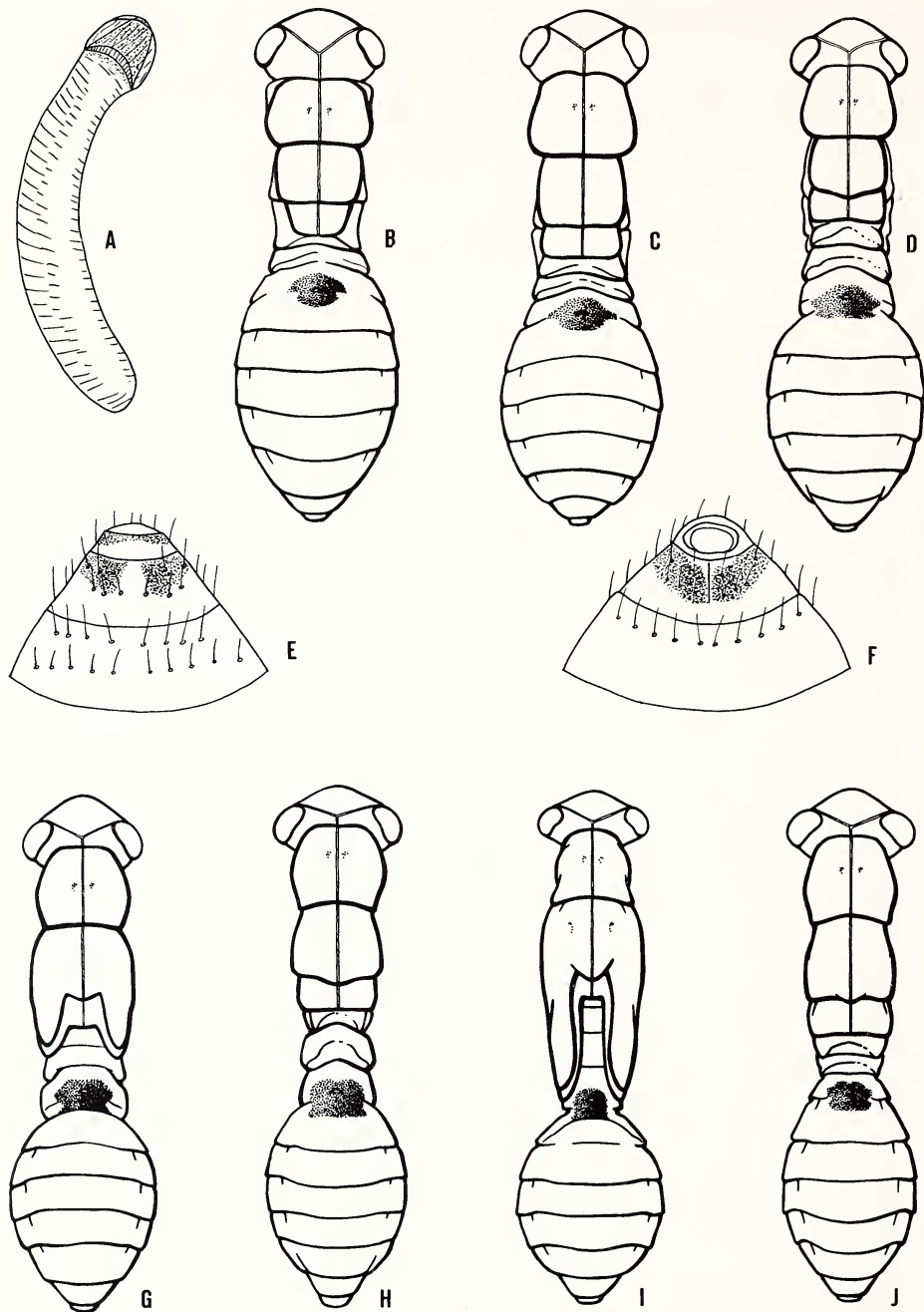


Fig. 5. Immature stages of *C. insignis*. a. Egg. b. First instar. c. Second instar. d-f. Third instar. d. Dorsal habitus. e. Ninth sternite of male. f. Ninth sternite of female. g, h. Fourth instar. g. Male. h. Female. i, j. Fifth instar. i. Male. j. Female.

neck; grayish white or pale brownish yellow; surface of corium smooth; anterior pole with simple, weakly convex chorionic operculum and large, distally tapered opercular process, both enclosed by thin chorionic rim collar.

NYPHS (Fig. 5b–j). The body regions of *insignis* nymphs are in large part weakly sclerotized. This is especially true of younger instars and of the abdomen of all stages. As a result, there is noticeable variation in the size and shape of the body, even between specimens of the same age. Abdomen shape is strongly influenced by the volume of food consumed and the length of time between feeding bouts. In illustrating the nymphs of *C. insignis*, we have selected alcohol-preserved specimens of average size and general shape, with no noticeable distortion of the various body regions. The five nymphal instars (see following descriptions) are most easily differentiated by overall length, size of the head capsule, length of the rostrum and second antennal segment, and for 3rd–5th instar males, the size of the wing pads (see Appendix 1 for comparative measurements). Sex can be determined down to the third instar by differential development of the sclerotized plates on the ninth abdominal sternite (Fig. 5e, f) and by the development of wing pads in the male.

FIRST INSTAR (Fig. 5b). Length 1.31–1.70 (measured from tip of tylus to apex of abdomen in lateral view; see Appendix 1 for other measurements); strongly myrmecomorphic, brown or reddish brown general coloration; abdomen pale, only lightly tinged with brown; head and thoracic nota shining, finely granulate; dorsum with sparsely distributed, short, black, bristle-like setae; antennae and legs with more densely distributed dark setae. Head: large, strongly declivous, subovate in lateral view, triangulate in frontal view; vertex strongly convex, posterior margin indistinct; frons weakly convex, strongly slanting anteriorly to weakly depressed junction with tylus; antennal fossa large, situated well anterior of eye; tylus short, moderately produced; jugum, lorum, and buccula short; gena and gula broad. Rostrum: reaching between metacoxae; segments I–IV similar in length. Antennae: brown, segment IV sometimes tinged with red; segment I short, barrel-shaped, slightly broader than II–IV; segments II and III linear, similar in length; segment IV slightly longer than II and III, tapered distally to narrowly rounded apex. Thorax: uniformly brown or dark brown; nota quadrate, pronotum slightly larger than mesonotum, these much larger than metanotum; pronotum with broadly rounded angles, lateral margins slightly sinuate, anterior margin weakly convex, posterior margin weakly concave; calli indistinct; meso- and metathoracic wing pads not developed. Abdomen: oblong-ovate, bulbous, segments I–III noticeably constricted; translucent, pale yellow or creamy white, sometimes lightly tinged with red; weakly sclerotized except for small sub-spherical disk surrounding external pore of dorsal abdominal scent gland (pore situated medially on suture between abdominal tergites III and IV). Legs: uniformly brown; tibiae with several rows of stout spines; tarsi two-segmented, segment I much shorter than II; pretarsal pulvillus large, reaching near apex of claw.

SECOND INSTAR (Fig. 5c). Very similar to first instar in structure and general coloration except larger (length 1.75–1.97), with distinctly longer and broader head (see Appendix 1 for measurements); pronotum slightly more rounded dorsally; abdomen usually more extensively tinged with brown or reddish brown, tergite IX heavily sclerotized; and sclerotized disk surrounding pore of abdominal scent gland larger.

THIRD INSTAR (Fig. 5d). Distinguished from earlier instars by larger body size

(length 2.43–2.75), longer and broader head, and much longer rostrum. Male with very small meso- and metathoracic wing pads; female with no wing pad development. Abdominal sternite IX of male with small, sclerotized plate either side of midline, plates broadly separated medially (Fig. 5e); female with pair of medially contiguous plates on ninth sternite (Fig. 5f).

FOURTH INSTAR. Male (Fig. 5g). Similar to third instar except larger (length 3.50–3.60), with much longer wing pads and rostrum. Mesothoracic wing pads reaching onto first abdominal sternite; rostrum reaching between mesocoxae or slightly beyond. Sclerotized plates on abdominal sternite IX considerably larger than in third instar, but remaining broadly separated.

Female (Fig. 5h). Similar to male in color and structure, except usually slightly smaller (length 2.80–3.60), with broader vertex and no development of wing pads. Distinguished from third instar female by its larger size, longer and broader head, and much longer rostrum and second antennal segment. Sclerotized plates on ninth abdominal sternite only slightly larger than in third instar.

FIFTH INSTAR. Male (Fig. 5i). Similar to fourth instar male except larger (length 4.40–4.80), with longer and broader head, larger eyes, antennal fossa narrowly removed from anterior margin of eye, and much longer rostrum, second antennal segment, and wing pads. Pronotum more trapezoidal with anterior angles very broadly rounded and posterior angles slightly upturned. Mesothoracic wing pads extending to posterior margin of third, or sometimes onto fourth abdominal tergite. Sclerotized plates on ninth abdominal sternite very large and only narrowly separated medially.

Female (Fig. 5j). Similar to male in color and structure except usually slightly smaller (length 4.35–4.55), with longer head, much broader vertex, and no development of wing pads. Distinguished from fourth instar female by larger body size, larger and broader head, and much longer rostrum and second antennal segment. Sclerotized plates on ninth abdominal sternite much larger than those of third and fourth instars.

Distribution and abundance. Although *insignis* would be considered a common myrmecomorphic mirid, its distribution is patchy among sites (Fig. 6). Of the 20 sites sampled in the Pike Creek drainage, *insignis* was common or abundant (maximum incidence equal to or greater than 0.50 per plant) at only six, which ranged in elevation from 1,577 m to 2,069 m. No individuals were collected at the lowest four sites, and because *L. caudatus* is limited to drier habitats, few *Coquillettia* individuals were found on the wetter north-facing slopes.

Dispersion within sites among single plants is approximated by a negative binomial model, indicating a clumped distribution (Fig. 8—Lloyd's mean crowding index increasing with mean density—Southwood, 1978). This clumping of individuals among plants may be explained in part by their propensity to select younger, larger, and better than average condition plants—these plant qualities also are dispersed aggregatively (McIver, pers. obs.).

Coquillettia was clearly the most abundant and widely distributed species of mirid on *L. caudatus* in the Pike Creek basin, with *Lopidea* nr. *rolfsi* (Orthotylinae: Orthotylini) the only other common mirid. *Coquillettia* represented 16.4% of all herbivorous insects collected on lupine at the CONF and PLAT sites over the 5-week period when it was most abundant (1 June to 5 July) (Table 2). The total numbers of *insignis* and Formicidae collected on 6,824 lupine plants over the entire field

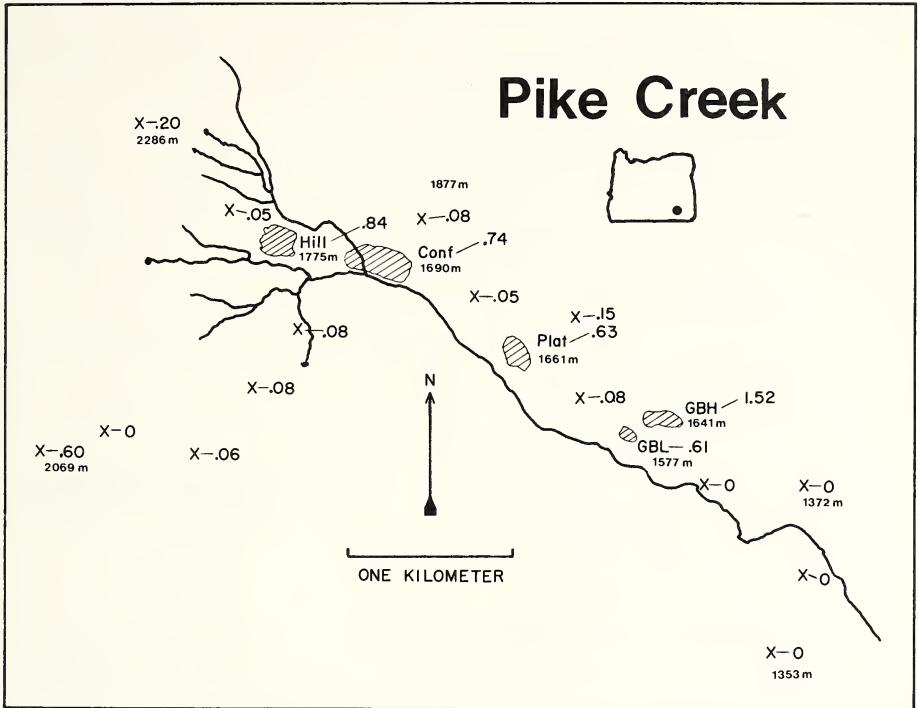


Fig. 6. Pike Creek drainage, southeastern Oregon. Hatched areas denote primary sites; proportions are maximum *C. insignis* numbers per plant from 23 May to 9 August 1985; elevations at selected sites in meters.

season (23 May to 11 July 1985) at all 20 sites were 1,346 and 1,627, respectively, indicating the abundance of this myrmecomorphic mirid relative to ants and other insects.

The pattern of abundance of *insignis* over time was influenced by elevation with abundance peaking earlier at the lower sites (GBL, GBH) than at the higher sites (CONF, HILL) (Fig. 9). Since elevation influences temperature regimes, both the host plant and *Coquillettia* populations will tend to develop later at higher, cooler sites. This observation is also reflected in regressions of deme developments over time for the five primary sites (Fig. 10). The differences in both slope and y-intercept among these regression lines are highly significant (ANAL. COVAR; $P < 0.01$), suggesting that speed of deme development is greater and mean hatching date is later at the higher sites. For example, at the HILL site, the population did not reach an index of 3.0 until 14 June, indicating that most or all of postembryonic development occurred during the warm month of June. After 14 June, the population required only 20 days to reach maturity, which is consistent with the estimate of 20.43 days obtained under optimal conditions of laboratory rearing at the BASE camp. Lower sites, like GBL and GBH, have populations that develop more slowly, probably

Table 2. Relative abundance of arthropod species collected on 3,625 *L. caudatus* plants from 1 June to 3 July 1985 at the CONF and PLAT sites, Pike Creek basin, southeastern Oregon.

Taxa	Abundance on 3,625 plants	Percentage of category
Herbivores		
<i>Coquillettia insignis</i> Uhler	641	16.4
<i>Lopidea</i> nr. <i>rolfsi</i> Knight	328	8.4
Other herbivores	2,930	75.1
Total herbivores	3,899	100.0
Formicidae [correspondence to <i>C. insignis</i> stadium]		
Dolichoderinae		
<i>Tapinoma sessile</i> (Say) [3rd]	28	4.3
Formicinae		
<i>Camponotus essigi</i> Smith [none]		
<i>Camponotus vicinus</i> Mayr [none]		
<i>Formica fusca</i> group [5th, AD]	27	4.1
<i>Formica haemorrhoidalis</i> [5th]		
<i>Formica neogagates</i> group [5th, AD]	332	51.0
<i>Formica obscuripes</i> Forel [AD]	41	6.3
<i>Lasius alienus</i> (Foerster) [3rd, 4th]		
<i>Lasius niger</i> (Linnaeus) [3rd, 4th]		
Myrmicinae		
<i>Aphaenogaster subterranea occidentalis</i> (Emery) [3rd, 4th]		
<i>Crematogaster mormonum</i> Emery [4th, 5th]	147	22.6
<i>Leptothorax nevadensis</i> Wheeler [3rd]	76	11.7
Total Formicidae (caught during sampling study)	652	100.0
Arthropod predators		
Araneae		
<i>Metaphidippus/Eris</i> sp.	2	0.6
<i>Misumena vatia</i> (Clerck)	2	0.6
<i>Misumenops celer</i> (Hentz) & <i>M. asperatus</i> (Hentz)	126	40.0
<i>Oxyopes scalaris</i> Hentz	17	5.4
<i>Phidippus</i> sp.	1	0.3
<i>Philodromus insperatus</i> Schick	2	0.6
<i>Sassacus papenhoei</i> G. & E. Peckham	33	10.8
<i>Synageles</i> sp.	2	0.6
<i>Thanatus</i> sp. imm.	8	2.7
<i>Tibellus chamberlini</i> Gertsch	7	2.4
<i>Xysticus montanensis</i> Keyserling	2	0.6
Hemiptera		
<i>Geocoris</i> sp. imm.	1	0.3
<i>Nabicula vanduzeei</i> (Kirkaldy) & <i>Nabis alternatus</i> <i>uniformis</i> Harris	47	14.7
<i>Phytocoris</i> sp. imm.	2	0.6
<i>Sinea diadema</i> (Fabricius)	32	10.1
Undetermined imm. Reduviidae	30	9.8
Total visual predators	312	100.0
Total non-visual predators	47	13.0

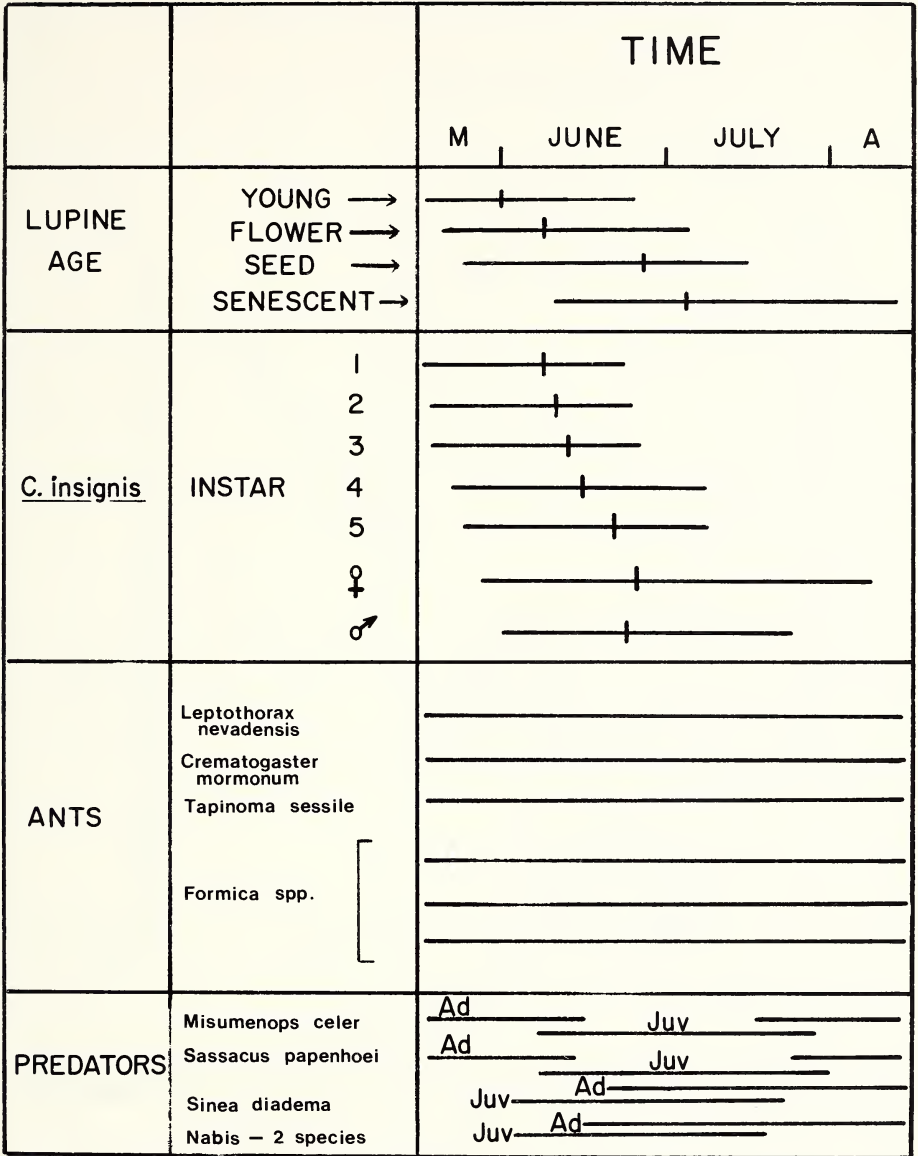


Fig. 7. Phenology of *L. caudatus*, *C. insignis*, and the primary ants and predators collected on lupine, 23 May-10 August 1985.

because much of postembryonic development occurs during the cooler month of May (Fig. 10).

Behavior. Thirteen individuals of *insignis* were observed continuously for 585 minutes in May, June and July 1985. Since behavior varied little among stadia,

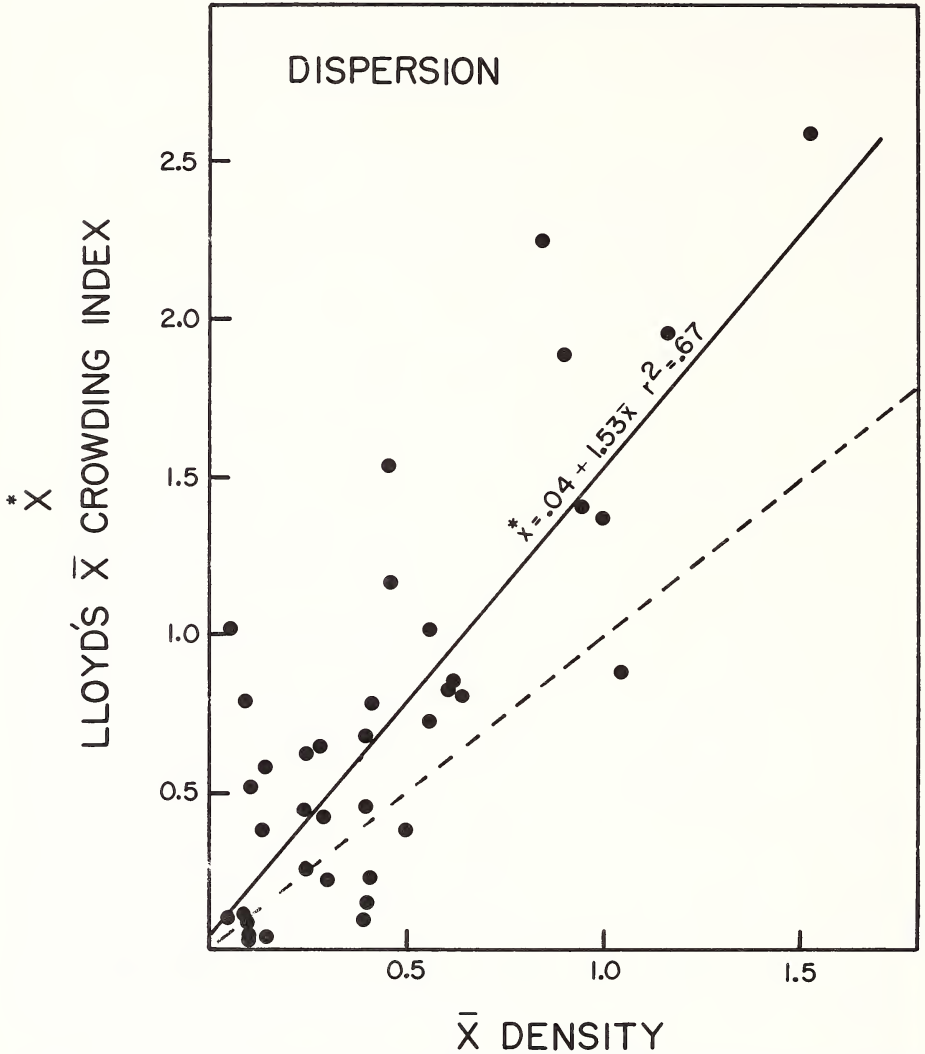


Fig. 8. Dispersion of *C. insignis* individuals among plants. Each point represents a sample characterized by a mean density (x-axis) and a mean crowding index (y-axis); dashed line is line of slope 1.

observational data are pooled in this analysis. Eight different behavioral activities were identified, excluding mating and oviposition (Fig. 11). The majority of active time was spent feeding (on flower primordia, leaflets, and seedpods) and in searching for appropriate food resource. Two types of searching were observed—a 'run-search' with the insect leaving a resource, tucking its proboscis in and hurrying to another resource patch, and 'probe-search,' with the insect proceeding at a much slower pace and using the proboscis to briefly sample potential resource patches. Feeding usually

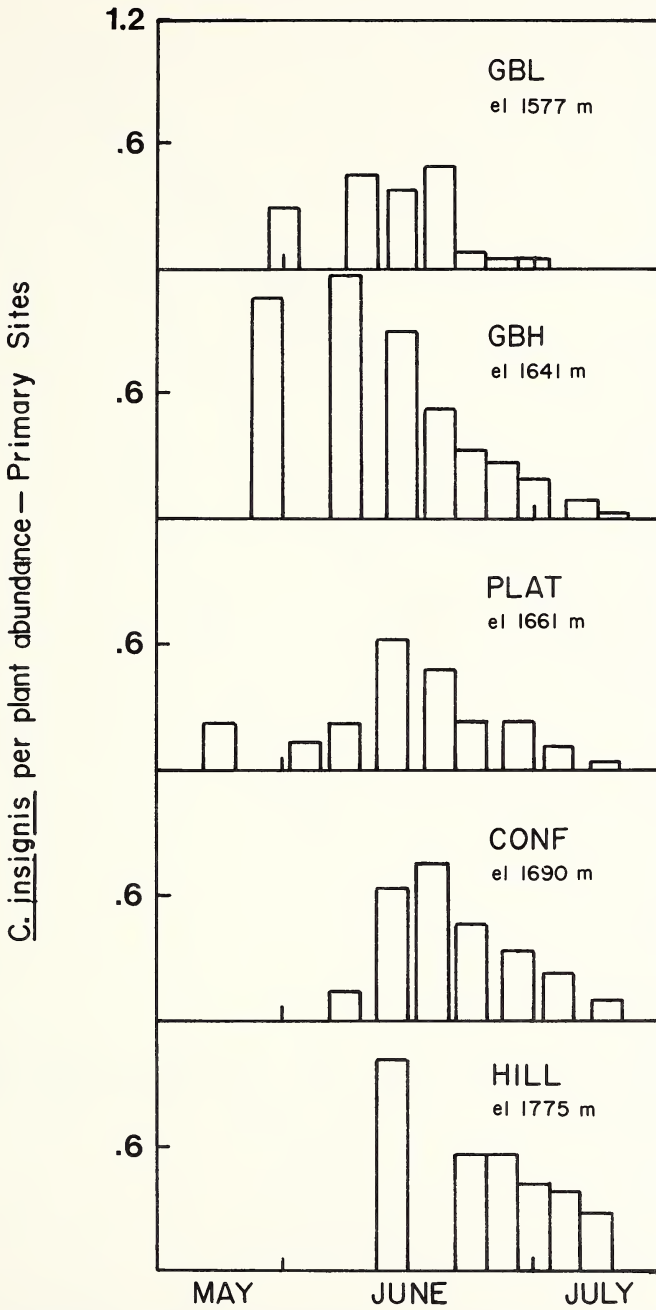


Fig. 9. Number of *C. insignis* individuals per lupine plant from late May to early July 1985, at the five primary sites in the Pike Creek drainage, southeastern Oregon.

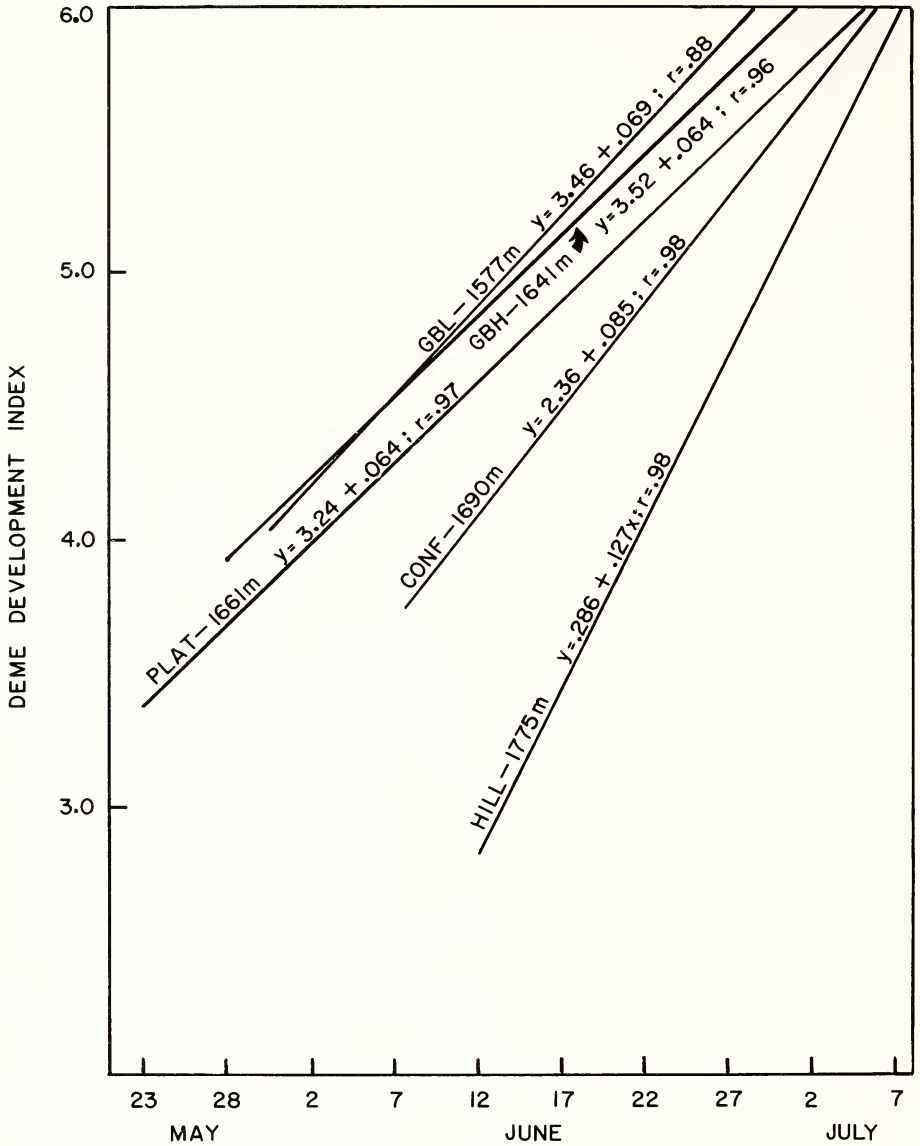


Fig. 10. Regressions of deme development index,

$$\left(\sum_{i=1}^6 n_i \cdot i \right) / N,$$

versus time for the five primary sites in the Pike Creek drainage, southeastern Oregon. All regressions are significantly different in y-intercept and slope (ANAL. of COVAR., $P < 0.01$).

involved a sequence of inserting the proboscis into plant tissue for a brief period of time (\bar{x} = 40.4 seconds per probe-feeding bout), probe-searching for a short distance, and then reinserting the proboscis. During this probe-feeding activity, the animal was always alert and responsive to outside stimuli, with both antennae gently swaying alternately. While probe-feeding constituted 29.8% of the total time budget, an animal occasionally (5.9% of total time) fed in a more intense manner, inserting the proboscis into the plant tissue for relatively longer lengths of time (\bar{x} = 102.7 seconds per feeding bout) and being much less responsive to outside stimuli. Only during this type of feeding behavior could the animal be approached and observed with a hand lens. No predatory behavior was observed, and it can be assumed that *insignis* is a visually oriented, relatively host specific diurnal herbivore.

The remainder of the time budget was consumed by 'resting' (16.9%) and 'grooming' (2.9%) behaviors. During the rest stage, the animal was alert and responsive, but immobile. Two types of rest were identified, an 'active' rest and a more passive rest. During active rest, the antennae would gently sway as in feeding, while during passive rest, all parts of the body were held motionless. Active rest typically occurred just after and just before another behavioral activity, while passive rest typically occurred between periods of active rest. Both types of rest generally took place on the underside of leaflets or stems, or in the stubble near the base of the lupine plant.

Grooming is a behavior undertaken by most insects and spiders and is necessary for keeping important body parts free of fouling material. *Coquillettia* individuals spent 2.9% of their active time in the grooming mode and were observed grooming the face, eyes, antennae, proboscis, and all three pairs of legs. Tarsi of the front pair of legs were used to groom all head-associated parts, while the 2nd and 3rd pairs of legs were usually rubbed against each other.

When this time budget is compared to budgets for two other mirid species (Fig. 11), some interesting patterns emerge. All three species spend a similar proportion of time grooming and feeding, two activities necessary for maintenance and growth. But the three species differ considerably in how they spend the rest of their time. *Lopidea* individuals spend over half of their time resting (58.5%), with very little time devoted to running (6.2%) and probing (0.4%). *Coquillettia* individuals run (29.8%) and probe (11.8%) more, but spend much less time resting (16.9%). The time budgeted to run and rest by *Orectoderus* individuals is intermediate to the values observed for *Lopidea* and *Coquillettia*. The same sequence (Lop-Orecto-Coq) is reflected in the extent to which these three species resemble ants morphologically. The non-myrmecomorphic *Lopidea* has a more typical plant bug shape with a relatively low length : width ratio (length measured from tip of tylus to apex of abdomen, width measured between 2nd and 3rd abdominal segments; $2.74 \pm 0.41 = 95\%$ conf. interval; $N = 9$). *Orectoderus*, a close relative of *Coquillettia*, is very ant-like, with a length : width ratio of $(4.47 \pm 0.33; N = 28)$. *Coquillettia* is even more linear ($6.55 \pm 0.35; N = 38$), and its morphological resemblance to ants more convincing than *Orectoderus* (see McIver and Stonedahl, 1987 for comparison). Behaviorally, *Lopidea* is much slower afoot than either *Orectoderus* or *Coquillettia*, with *insignis* clearly the quickest of the three. The speed at which individuals of *insignis* conduct various behavioral activities is reflected in the time budgets, with a greater proportion of time spent run-searching and a lesser amount of time spent resting relative to the other species. Moreover, estimates of behavioral changes per minute and distance

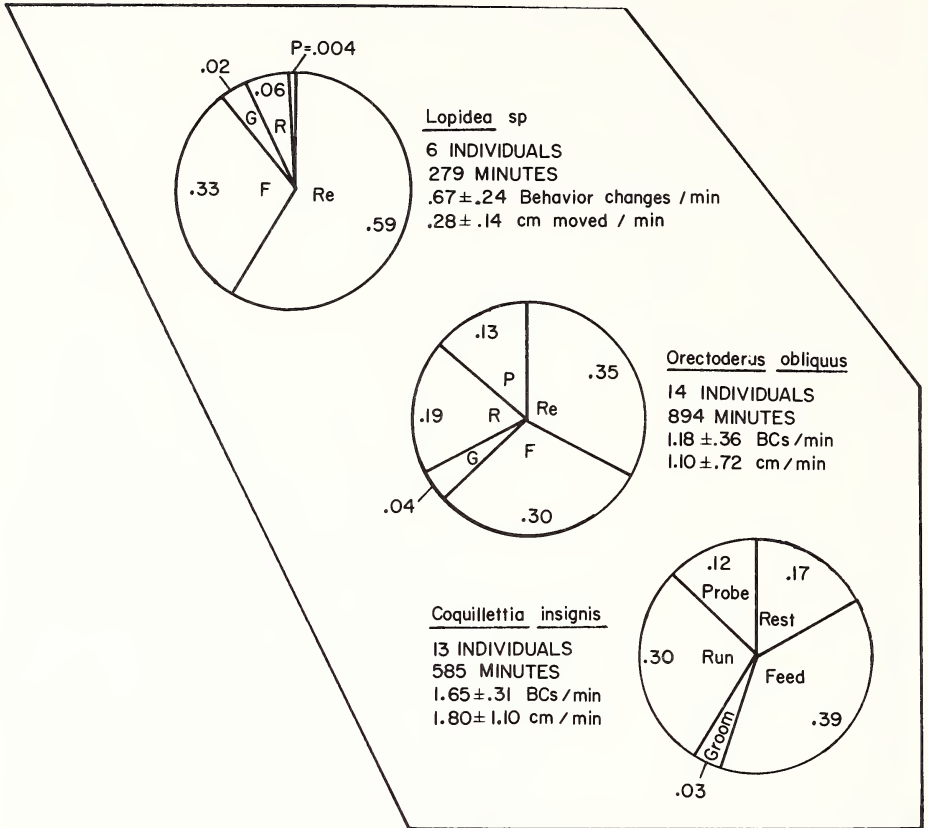


Fig. 11. Relative proportion of time spent in five behavioral categories for *Lopidea* nr. *rolfsi*, *Orectoderus obliquus*, and *Coquillettia insignis*. Observations of *Orectoderus* made July–August 1984, H. J. Andrews Experimental Forest, central Cascades, Oregon; observations on *Lopidea* and *Coquillettia* made May–July 1985, Pike Creek drainage, southeastern Oregon.

moved per minute both indicate that *Coquillettia* is generally more frenetic during its active period (Fig. 11). This frenetic behavior, coupled with its morphology, makes *insignis* a very convincing myrmecomorph, since ants are generally both linear and quick afoot (McIver, 1987).

One instance of territoriality between adult females was observed, with the defended resource being flower primordia. In this incident, two females were engaged in a confrontation for approximately 15 minutes, where the larger of the pair succeeded in preventing the smaller from using a cluster of flower primordia by chasing and making aggressive contact with the front legs. The smaller female was driven off six times within the 15-minute period.

Possible ant models. Twelve ant species were collected on or around lupine by sweep-net, beat-sheet, and pitfall trap over the 10-week study period (Table 2). Six species occurred commonly on lupine, with the rank order of abundance *Formica*

neogagates group—*Crematogaster mormonum* Emery—*Leptothorax nevadensis* Wheeler—*Formica obscuripes* Forel—*Tapinoma sessile* (Say)—*Formica fusca* group. These ant species differ considerably in size, shape, color, and behavior, and so the correspondence between these species and *Coquillettia* individuals can only be described in general terms: there is no single ant-like morphology or behavior that would serve as a specific model toward which ant-mimics might evolve.

The three common *Formica* species are large, fast, and relatively aggressive, and might serve as general models for the 4th and 5th instar *Coquillettia* nymphs, and the adult female. Although the *Formica* species have much larger heads than similarly-sized *Coquillettia*, the overall body correspondence between models and mimic is remarkably close. Moreover, running behavior is much the same in the *Formica* species and adult female of *Coquillettia* (see McIver, 1987), making field discrimination difficult.

Further, the adult female of *insignis* is polymorphic in general coloration, with a graded series of RED/BLACK to BLACK morphs occurring in most populations. The common morph is black, by a ratio of 3:1 (211:79) over sites where both extremes are abundant. The three common *Formica* species that correspond to adult females in size can be found at the same sites as the myrmecomorph with body colorations closely approximating the two morphs of *Coquillettia*. The red *Coquillettia* morph and *F. obscuripes* are both red on the head, antennae, and thorax, and dark brown on the abdomen, with the only difference being the legs (rusty red for *Coquillettia* and dark brown for *F. obscuripes*). The black *Coquillettia* morph, as well as *Formica fusca* group and *F. neogagates* group, are dark brown to black on the head, thorax, legs, and abdomen, and red on the antennae. We have observed similar patterns of color-polymorphism in other species of *Coquillettia*, as well as in other genera of ant-like Miridae (e.g., *Orectoderus*, *Paradacerla* Carvalho and Usinger). Whether these correspondences represent fine-tuned mimetic adaptations or mere coincidence is unknown.

The two common myrmecines, *Crematogaster mormonum* and *Leptothorax nevadensis*, have very different morphologies and behaviors when compared to the *Formica* species and to *Coquillettia*. Both are relatively slow moving for ants and run in a smooth, nonstopping manner, unlike *insignis*. They are typically docile and usually found near lupine blooms and seed pods, as opposed to other parts of the plant. *Leptothorax* is matched by 3rd instar *insignis* in size, but is much more linear and different in color, with the thorax and abdomen red and brown, respectively, the opposite of *insignis* nymphs. *Crematogaster* is matched by 4th instar nymphs in size, but has a much larger head and wider abdomen than nymphs of similar size. The only body part of *mormonum* showing the same coloration as in *insignis* nymphs is the brown head.

The dolichoderine *Tapinoma sessile* is a small, docile ant that is matched very closely by 3rd instar *insignis* nymphs. The size ranges for 3rd instar nymphs and *T. sessile* individuals are almost identical and the shape of the dorsal profile very similar because of the relatively small head of this ant. Coloration is the same for all body parts except the abdomen (brown for *Tapinoma* and pale with a reddish tint for *Coquillettia* nymphs).

No common ants of appropriate size were found that could potentially serve as models for the 1st or 2nd instar nymphs of *C. insignis*.

Predators/operators. Most available data suggest that the resemblance between ants and solitary myrmecomorphic arthropods like *Coquillettia* is Batesian mimicry, where the mimic resembles a distasteful or dangerous model, is confused with it by visual predators, and gains protection by being avoided significantly more often (Rettenmeyer, 1970; Reiskind, 1977; Oliveira and Sazima, 1984; McIver, 1987). The most common predators that occur on lupine are visual insects (reduviids and nabids) and spiders (salticids, thomisids, philodromids, oxyopids). Nonvisual arthropod predators constituted only 13.0% of the total abundance of predators collected on lupine over the 5-week period of peak *Coquillettia* abundance (Table 2). Other possibly important predators observed were three species of lizards (collared, western-fence, side-blotched) and five principal species of birds (green-tailed towhee, lazuli bunting, rock wren, canyon wren, sage sparrow). Any or all of these visual invertebrate or vertebrate predators could potentially maintain a tripartite ant-mimicry system, involving both *Coquillettia* and its various ant models. We have evidence that species in at least two major families of arthropod predators (Reduviidae, Salticidae) classify *Coquillettia* individuals with ants, rather than with nonmimetic Miridae (McIver, 1987). Our data suggest that the role of visual arthropod predators in maintaining ant-mimetic systems has been underestimated and requires further investigation.

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APPENDIX 1

Table of ranges and means of six measurements (in millimeters) for the nymphs and adults of *C. insignis*. Nymphal measurements were taken from alcohol-preserved specimens; adult measurements from dried specimens; N = 4.

Stage	Tot. length ¹	Head		Ant. seg. II	Rostrum	Mesothoracic wing pad
		Length	Width ²			
1st instar	1.31-1.70	0.40-0.44	0.34-0.37	0.29-0.35	0.61-0.65	0
	1.51	0.42	0.35	0.30	0.63	0
2nd instar	1.75-1.97	0.50-0.56	0.42-0.45	0.42-0.46	0.70-0.78	0
	1.85	0.54	0.43	0.45	0.75	0
3rd instar	2.43-2.75	0.71-0.75	0.58-0.62	0.66-0.72	1.01-1.04	0.06 ³
	2.56	0.72	0.60	0.69	1.02	0.06
4th instar						
Male	3.50-3.60	0.85-0.91	0.72-0.75	0.93-1.00	1.25-1.29	0.25-0.30
	3.55	0.88	0.74	0.96	1.27	0.28
Female	2.80-3.60	0.88-0.98	0.71-0.78	0.91-1.00	1.19-1.39	0
	3.14	0.93	0.74	0.96	1.31	0
5th instar						
Male	4.40-4.80	1.00-1.10	0.87-0.90	1.46-1.60	1.54-1.60	0.94-1.60
	4.63	1.05	0.89	1.50	1.57	1.02
Female	4.35-4.55	1.17-1.20	0.91	1.40-1.48	1.64-1.70	0
	4.43	1.19	0.91	1.44	1.67	0
Adult male	4.50-5.15	1.05-1.14	0.90-0.97	1.89-2.32	1.70-1.86	—
	4.74	1.09	0.93	2.14	1.79	—
Adult female	4.45-5.30	1.29-1.56	0.96-1.12	1.88-2.15	1.71-2.01	—
	4.88	1.43	1.04	2.03	1.84	—

¹ Measured from tip of tylus to apex of abdomen.

² Measured across eyes in dorsal view.

³ Male only.